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Tropical land-sea couplings: Role of watershed deforestation, mangrove estuary processing, and marine inputs on N fluxes in coastal Pacific Panama

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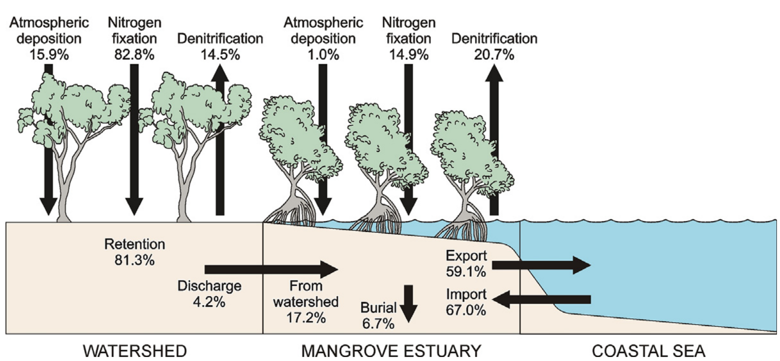
HIGHLIGHTS

- Connectivity of watersheds, mangrove estuaries and adjacent coastal seas was assessed.
- Only a small fraction of nitrogen entering watersheds reaches mangrove estuaries.
- Estuary inputs and losses are matched, and nitrogen exports subsidy coastal food webs.
- Forest cover modulates the magnitude of nitrogen inputs, interception and discharges.

GRAPHICAL ABSTRACT



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ABSTRACT

We review data from coastal Pacific Panama and other tropical coasts with two aims. First, we defined inputs and losses of nitrogen (N) mediating connectivity of watersheds, mangrove estuaries, and coastal sea. N entering watersheds—mainly via N fixation (79-86%)—was largely intercepted; N discharges to mangrove estuaries (3-6%), small compared to N inputs to watersheds, nonetheless significantly supplied N to mangrove estuaries. Inputs to mangrove estuaries (including watershed discharges, and marine inputs during flood tides) were matched by losses (mainly denitrification and export during ebb tides). Mangrove estuary subsidies of coastal marine food webs take place by export of forms of N [DON (62.5%), PN (9.1%), and litter N (12.9%)] that provide dissimilative and assimilative subsidies. N fixation, denitrification, and tidal exchanges were major processes, and DON was major form of N involved in connecting fluxes in and out of mangrove estuaries. Second, we assessed effects of watershed forest cover on connectivity. Decreased watershed forest cover lowered N inputs, interception, and discharge into receiving mangrove estuaries. These imprints of forest cover were erased during transit of N through estuaries, owing to internal N cycle transformations, and differences in relative area of watersheds and estuaries. Largest losses of N consisted of water transport of energy-rich compounds, particularly DON. N losses were similar in magnitude to N inputs from sea, calculated without considering contribution by intermittent coastal upwelling, and hence likely under-estimated. Pacific Panama mangrove estuaries are exposed to major inputs of N from land and sea, which emphasizes the high degree of bi-directional connectivity

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Dissolved organic nitrogen
Litterfall

in these coupled ecosystems. Pacific Panama is still lightly affected by human or global changes. Increased deforestation can be expected, as well as changes in ENSO, which will surely raise watershed-derived loads of N, as well as significantly change marine N inputs affecting coastal coupled ecosystems.

1. Introduction

Quantifying the complex couplings between tropical watersheds, down-gradient mangrove estuaries, and coastal seas is a challenging problem (McKee et al., 2000; Borbor-Cordova et al., 2006; Eyre and Maher, 2011; Eyre et al., 2011; González-De Zayas et al., 2013). Revealing degree, direction, and controls of connectivity in coupled ecosystems is made difficult because of the many processes involved, contrasting responses of diverse materials involved in couplings, and differences in function among the coupled ecosystems.

One approach to issues in coastal connectivity in temperate coastal systems has been through understanding sources, fate, and discharge of nutrients from adjoined land-water ecosystems (Valiela et al., 1992; Nixon et al., 1995; Galloway et al., 1996; Howarth et al., 1996; Voss et al., 2011; Jorgensen et al., 2014; Bryhn et al., 2017). An early example is the long-held outwelling hypotheses that engendered thinking about inter-ecosystem connectivity (Lee, 1995). In tropical coastal systems, some papers dwell on land-to-mangrove estuary linkages (Gleeson et al., 2013; Makings et al., 2014), and many others assess export from mangrove estuaries to coastal waters (Lee, 1995, Dittmar et al., 2001, Mfilinge et al., 2005, Bouillon et al., 2008, Adame and Lovelock, 2011, Walton et al., 2014, Gillis et al., 2015, Reis et al., 2017, among others). Here we develop an assessment of the series of couplings among coastal watersheds, mangrove estuaries, and coastal seas. We focus on nitrogen (N) fluxes because this element regulates many aspects of functioning of coastal ecosystems (Sections 3.2 and 17.2 in Valiela, 2015).

1.1. Connected ecosystems: watersheds, mangrove estuaries, and coastal sea

Below we review available evidence on N fluxes obtained by us in coupled coastal environments on the Pacific coast of Panama, supplemented as needed by meta-analysis of results from other similar regions, with two aims: 1) define magnitude, controls, and mechanisms involved in connections of coupled tropical coastal ecosystems; and 2) assess whether the widespread deforestation of tropical terrestrial watersheds affects connectivity among coastal environments.

In the Pacific coast of Panama, as in many other places throughout the tropics, there are three potentially connected coastal ecosystems: 1) *terrestrial watersheds* that receive N inputs from atmospheric deposition and net gaseous N exchanges, and discharge N to the edge of mangrove estuaries; 2) *mangrove estuaries*, environments consisting of shallow un-vegetated waterways through which tidal water travels twice a day in and out of the much more extensive mangrove-covered areas; these mangrove estuaries receive land-derived and atmospheric N, are sites of net gaseous exchanges, sequestration of N in sediments, and of exchange of N with coastal waters; and 3) *coastal sea* that receives N from estuary discharges, and potentially contributes marine-derived N to mangrove estuaries.

To ascertain the degree of connectivity between the three adjoined ecosystems, and test the hypotheses that tropical watersheds retain the bulk of their N inputs, and that N retention governs connections to down-gradient receiving mangrove estuary ecosystems., below we first obtain best estimates of N inputs and losses to and from watersheds of Pacific Panama, and then estimate N retention and exports in and from watersheds.

N discharged from watersheds into receiving mangrove estuaries is subject to further transformations down estuarine gradients (Alongi, 1998, Sánchez-Carrillo et al., 2009, Adame et al., 2010 Potter et al., 2010, Eyre et al., 2011, Smith et al., 2012, Valiela et al., 2013a, among others). Most studies conclude that the bulk of externally derived N is retained or intercepted within mangrove estuaries, so that mangroves act as “filters” that protect coastal waters from larger loads of land-derived exports such as nitrate (Dittmar and Lara, 2001; Bruijnzeel, 2004; Ramos e Silva et al., 2007; Valiela et al., 2013, 2013a; Reis et al., 2017). A few studies, instead, find that mangrove estuaries add N to their exports (Talane-McManus et al., 2001; Mukhopadhyay et al., 2006), but comparisons among the different published studies are difficult, because few studies comprehensively include inorganic, organic, and particulate forms of N, each of which can be significant or dominant in different sites. Understanding within-mangrove estuary retention is a key feature that could uncouple connectivity of watersheds, mangrove estuaries, and coastal seas. Below we test the estuarine retention hypothesis by a review of results that comprehensively include the various forms of N in eight watershed-mangrove estuaries in Pacific Panama (Fig. 1, and Valiela et al., 2013, 2013a, 2014), combined with results from other publications.

Although significant N interception within most mangrove estuaries is likely, some fraction of the N does manage to course through mangrove estuaries, and is exported to receiving coastal waters (Jennerjahn and Ittekkot, 2002; Dittmar et al., 2006; Kristensen et al., 2008). Most tropical coastal marine waters are rather nutrient-poor, so that export of even a minor fraction of N compounds from mangrove estuaries to sea could establish connectivity to coastal ecosystems, since such export may add biologically significant amounts of N and energy-containing materials to coastal food webs (Boto and Bunt, 1981; Boto and Wellington, 1988; Valiela et al., 2013). Below we assess, for Pacific Panama as an example case, the degree of connectivity contributed by N exports from mangrove estuaries to coastal sea.

In general, tropical surface waters are N-poor, so that the inputs of marine N into mangrove estuaries may be minor, but we hypothesize that marine N inputs to mangrove estuaries may be quantitatively significant, as argued for temperate systems (Riley, 1967; Nixon et al., 1995). In certain coasts, global- or regional-scale scale climate drivers may have pronounced effects, likely interacting with local-scale watershed-derived deforestation effects. One such large-scale climate-driven process that seems important in regions such a Pacific Panama are intermittent geostrophic upwelling (Rodríguez-Rubio et al., 2003; D'Croz and O'Dea, 2007; Pennington et al., 2006; Camilli et al., 2007), that brings up water bearing concentrations >20 μM DIN to the surface from below 30 m (Pennington et al., 2006; D'Croz and O'Dea, 2007). These intermittent hydrographic events may sustain relatively higher N concentrations in surface water than usually found in tropical oceanic waters, which in turn can be then be driven into mangrove estuaries by tidal forcing (Valiela et al., 2013, 2013a). To test the hypothesis that marine inputs are significant, and assess the magnitude of this sea-to-mangrove estuary connection—a reversal of the usual land to sea direction of connectivity—below we estimate inputs of marine-derived N into the Pacific Panama mangrove estuaries.

1.2. Effects of Watershed Deforestation on Connectivity and Down-gradient Fate of N

Deforestation of tropical landscapes is increasing (Wassenaar et al., 2007; Scanlon et al., 2007), often owing to conversion of forest to pasture land covers. Such shifts of land cover in turn can change N retention